

Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert

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Abstract

Biological soil crusts (cyanobacteria, mosses and lichens collectively) perform essential ecosystem services, including carbon (C) and nitrogen (N) fixation. Climate and land-use change are converting later successional soil crusts to early successional soil crusts with lower C and N fixation rates. To quantify the effect of such conversions on C and N dynamics in desert ecosystems we seasonally measured diurnal fixation rates in different biological soil crusts. We classified plots on the Colorado Plateau (Canyonlands) and Chihuahuan Desert (Jornada) as early (*Microcoleus*) or later successional (*Nostoc/Scytonema* or *Placidium/Collema*) and measured photosynthesis (P_n), nitrogenase activity (NA), and chlorophyll fluorescence (F_v/F_m) on metabolically active (moist) soil crusts. Later successional crusts typically had greater P_n , averaging 1.2–1.3-fold higher daily C fixation in Canyonlands and 2.4–2.8-fold higher in the Jornada. Later successional crusts also had greater NA, averaging 1.3–7.5-fold higher daily N fixation in Canyonlands and 1.3–25.0-fold higher in the Jornada. Mean daily F_v/F_m was also greater in later successional Canyonlands crusts during winter, and Jornada crusts during all seasons except summer. Together these findings indicate conversion of soil crusts back to early successional stages results in large reductions of C and N inputs into these ecosystems.

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1. Introduction

Dryland ecosystems cover roughly 35% of the western US, and over 35% of the global terrestrial land mass. These ecosystems are experiencing a significant increase in a wide range of human uses, including livestock grazing, agriculture, energy exploration, recreation, military training and urbanization. Soil surface disturbances associated with these uses have been repeatedly shown to convert species-rich biological soil crusts, dominated by late successional cyanobacteria and lichens, to species-poor crusts dominated by early successional cyanobacteria (reviewed by Belnap and Eldridge, 2003). Climate change is likely to further exacerbate this conversion of later successional to early successional crusts. Increasing summer temperatures have been linked to a dramatic decline in the abundance and physiological functioning of the later successional lichen *Collema*, and the cyanobacteria *Nostoc* and *Scytonema* (Bowker et al., 2002; Belnap, Phillips and Troxler, unpublished). Increased summer precipitation has been linked to a decline in cover and physiological performance in *Collema* on both the Colorado Plateau (Belnap et al., 2004) and Mojave Desert (J. Zimpfer, pers. comm.).

Collectively, biological soil crusts perform vital ecosystem services, however, differences in species abundance and composition affect the rate and type of these services. Early successional cyanobacteria (*Microcoleus*) soil crusts in arid and semi-arid regions are light in color, have little UV-protective pigmentation and low biomass (Belnap et al., 2003). As biomass increases, the dark-colored later successional, but relatively immobile cyanobacteria (e.g. *Nostoc* spp., *Scytonema* spp.) colonize. Lichens and mosses, also darkly colored with UV-protective pigments, are next to colonize. Several of these pigments (e.g. canthaxanthin, β -carotene, scytonemin, etc.) are important for dissipating ultraviolet energy penetrating crust organisms, thereby preventing damage to PS II reaction centers and protein complexes (Castenholz and Garcia-Pichel, 2000), hence higher quantum yield is expected in later successional crusts. Due to their dark color later successional crusts may increase soil temperatures, resulting in more rapid rates of soil nutrient transformation and uptake by plants. The greater biomass of later successional crusts also better stabilizes soils against wind and water erosion (Belnap and Gillette, 1997; McKenna-Neumann and Maxwell, 1999; Warren, 2003), thus preserving soil fertility.

Carbon (C) and nitrogen (N) fixation capabilities vary with the abundance and species composition of a given biological crust type, as well as temperature and hydration history (Jeffries et al., 1993; Lange, 2003). Rates of C fixation by *Microcoleus* dominant crusts are generally low ($\sim 1 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), due to their lower overall cyanobacterial biomass and chlorophyll content (Garcia-Pichel and Belnap, 1996), and limited light penetration to the region they occupy below the soil surface (Lange, 2003). Conversely, crusts with abundant lichens and mosses on the soil surface are capable of photosynthetic rates $> 10 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (Lange, 2003). Prior environmental conditions influence nitrogenase activity (NA, as measured by ethylene production), as crusts that have been hydrated more recently are presumed to have greater amounts of ATP and nitrogenase available upon rewetting, and hence greater NA than those that have been desiccated for a longer period of time (Belnap, 2003). Species composition and abundance is also likely to be very important in determining NA, as laboratory measures have shown the later successional species *Collema*, *Nostoc* and *Scytonema* to have much higher rates of N fixation than *Microcoleus* (Belnap, 2002). Hydration is the key control over C fixation, and

hence N fixation by these organisms, so the ability to remain hydrated at the soil surface ultimately determines fluxes of C and N.

In this study we examined the response of C and N fixation rates to wetting in successional stages of biological soil crusts from the relatively cool Colorado Plateau and warm Chihuahuan Desert. Hydrating the crusts was necessary to measure rates of C and N fixation, as biological soil crusts are inactive when dry. Comparison of C and N fixation was not possible between locations, as these processes are dependent on temperature and the relative abundance of different crust species, both of which differed between Canyonlands and the Jornada. However, by comparing crust types within sites we hope to better understand how the current and predicted future decline of later successional crust types may affect C and N inputs into these ecosystems. We measured photosynthesis, N fixation, and chlorophyll fluorescence seasonally over a diurnal time course, predicting that later successional soils crusts would have higher rates of photosynthesis and N fixation, and higher F_v/F_m values than less developed soil crusts, regardless of origin.

2. Materials and methods

2.1. Site description and sampling characteristics

The cold desert Canyonlands site in SE Utah (38°35.08'N, 109°49.16'W) was located on a Rizno loamy mixed, calcareous soil and characterized as pinyon-juniper woodland containing *Pinus edulis*, *Juniperus osteosperma*, and *Coleogyne ramosissima*. Early successional crusts from this site used for C and N fixation lacked mosses and lichens, and the predominant cyanobacterium was *Microcoleus* (83% relative cover). Later successional crusts had greater relative cover of the cyanobacteria *Nostoc* and *Scytonema* (32% combined). These crusts also contained 7% lichen (3% *Fulgensia desertorum*, 2% *Collema tenax*, 1% each of *Aspicillia hispida*, *Placidium squamulosum*) and 1% *Syntrichia caninervis* cover as determined by the point-intercept method (50 points per 137 cm² sample). For NA measurements, patches of *Collema* were avoided as this species has very high N fixation (Belnap, 2002). This was done so that our measures would be more compatible with other sites and studies that lack this species. Therefore, NA measures obtained in this study are conservative for these sites.

The warm desert Jornada Experimental Range site in southern New Mexico (32°31.80'N, 106°43.41'W) was located on a Regan clay loam soil with *Flourensia cernua* the dominant shrub. Early successional crusts again lacked lichens and mosses, and were dominated by *Microcoleus* (93% relative cover). Later successional crusts had greater relative cover of *Nostoc* and *Scytonema* (40% combined), and contained the lichens *P. squamulosum* (19%), *C. coccophorum* (11%), *P. lachneum* (6%) and *Heppia lutosa* (2%). For NA measurements, similar later successional crusts were used, with *Collema* again intentionally avoided.

At both sites, three 15-cm diameter PVC soil collars were inserted ~5 cm into the soil around each crust type. Gas exchange measurements were taken on clear days when the sites had not received any rainfall in the past 72 h. Because biological soil crusts are inactive when dry, 2 h prior to measurement each collar was hydrated with ~150 ml of distilled water, and then kept moist throughout the day to determine C and N fixation rates on active (i.e. moist) crusts. Net photosynthesis (P_n) and chlorophyll fluorescence (F_v/F_m) were measured every 2–3 h from sunrise to sunset. Gas exchange measurements

were made using a Licor 6400 portable photosynthesis system with a custom chamber that fit directly over the soil collar. Natural light was transmitted (>93%) through the 137 cm² clear polycarbonate chamber top, and air temperature remained within 3 °C of ambient conditions. After system stabilization we measured gross photosynthesis (P_g) in the light, then an opaque cover was placed over the collar to determine respiration. Measurements in the light include heterotrophic respiration of underlying soil organisms and photorespiration (i.e. ecosystem respiration; R_e), but photosynthesis ceased shortly after inhibiting PAR, allowing us to measure R_e , which subtracted from P_g , gave P_n of the soil crust. These photosynthetic rates were calculated on a surface area basis as $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$. From this data we then calculated daily P_n by integrating the area under the diurnal curves using Sigmaplot (Systat Software Inc., USA).

Within minutes after measuring R_e we measured dark-adapted chlorophyll fluorescence (F_v/F_m) using a PAM-2000 portable fluorometer (Walz, Germany). A saturating pulse of light was delivered under the opaque cover at three different points per soil collar and the values averaged. A distance clip ensured each pulse was delivered at the same height (~5 mm) above the crust surface.

Nitrogenase activity was measured in the field at each site by seasonally collecting 3 cm deep cores in 2.5 cm diameter clear polycarbonate tubes with >93% light transmission ($n = 6-8$ per crust type). Samples were wetted with ~3 ml of water as previously described, then each tube was sealed with a rubber stopper to form an airtight chamber, and injected via a septa with enough acetylene to create a >10% acetylene atmosphere. Temperatures within the tubes remained within 5 °C of ambient conditions. After 60–90 min, 4.0 ml of headspace was withdrawn from each tube and injected into a vial. This process was repeated throughout the day to coincide with gas exchange measurements. Between samplings the top stopper was removed to allow the headspace to mix with outside air. Samples were analysed on a Shimadzu gas chromatograph (Kyoto, Japan) equipped with a Hayesep-T column, using N₂ as the carrier gas. Results were expressed as ethylene production per unit time on a surface area basis ($\mu\text{mol C}_2\text{H}_4\text{m}^{-2}\text{h}^{-1}$). From these diurnal data, we then determined daily integrated ethylene production as described above for photosynthesis.

Upon completion of each diurnal sampling period, crust samples used for NA analyses were dried and the top 5 mm were removed to quantify cyanobacterial taxa. In order to have enough material for these analyses, two samples from each crust type were randomly paired and pooled, giving $n = 3-4$ samples per crust type. The samples were ground with a Mixermill 200 (Retsch, Germany) for 10 min at 27 Hz, then 0.5 g was taken from each sample and mixed with 2 ml distilled water. Four subsamples consisting of 2 drops were placed onto microscope slides, and then 10 random views per slide were observed using a compound microscope at 300X power. The percentage of each field of view occupied by each cyanobacterial taxa was recorded, then relative cover of each taxon calculated.

2.2. Data analyses

The diurnal data were first analysed separately by season and site using the repeated-measures ANOVA procedure of SAS (1989). The dependent variables were P_n , NA and F_v/F_m , while crust type, time of day (hereafter time) and their interaction were model effects. When the assumptions of ANOVA could not be met through transformation of the data, we used Friedman's χ^2 to examine the dependent variable by crust type while

controlling for time (Sokal and Rohlf, 1997), followed by a Wilcoxon Two-Sample test to examine the dependent variable by the main effects crust type and time. Next, for each site we used ANOVA's to compare the daily integrated photosynthesis and ethylene production of crust types within seasons. These daily integrated parameters for each crust type differ from the repeated measures parameters for each crust type in that the former measure total values for the day while the latter measure average daily values. Our cyanobacterial relative cover data were similar seasonally, so for each site we pooled the seasons by crust type to increase sample sizes, and then tested differences between crust types within sites using Wilcoxon Two-Sample tests. Jornada cyanobacterial relative cover analysis did not include spring and fall data due to accidental destruction of samples.

Statistical tests of C and N fixation measurements were not made between sites or seasons due to differences in relative species abundance, temperature, humidity, and other factors that confound the interpretation of results. Due to the inherent variability in these crusts and the necessarily small sample sizes due to time constraints, we report $p < 0.10$ as significant unless otherwise indicated.

3. Results

Fifty-year (1954–2003) average annual temperatures near the Canyonlands and Jornada sites were 14.0 and 14.6 °C, with average winter temperature 3.0 °C cooler in Canyonlands. Over this period, annual precipitation averaged 211 and 252 mm, respectively. During the period of study (May 2003–March 2004) temperatures were warmer (14.8 °C Canyonlands, 15.3 °C Jornada) and precipitation lower (Canyonlands 163 mm, Jornada 101 mm) than the long-term averages.

Cyanobacterial species relative cover differed significantly between crust types within each site. Early successional crusts at both Canyonlands and Jornada had greater percent cover of *Microcoleus* and lower percent cover of *Nostoc* compared to the later successional crusts at a given site (Table 1). At the Jornada, later successional crusts had significantly greater percent cover of *Scytonema* than early successional crusts.

C fixation, when dissimilar, was greater in later versus early successional soil crusts. Repeated-measures ANOVA indicated significant differences in diurnal P_n by crust type in Canyonlands during spring and summer, but no significant crust type \times time interactions for diurnal P_n during any season (Table 2). However, all seasons did have significant time effects on P_n , with lower photosynthetic rates in early morning versus midday in

Table 1

Cyanobacterial composition of early and later successional biological soil crusts of the Colorado Plateau (Canyonlands) and Chihuahuan Desert (Jornada)

Cyanobacteria	Canyonlands			Jornada		
	Early successional	Later successional	<i>n</i>	Early successional	Later successional	<i>n</i>
<i>Microcoleus</i> (%)	82.7 _a (3.1)	68.0 _b (4.7)	15	93.1 _a (0.9)	60.3 _b (8.6)	8
<i>Nostoc</i> (%)	15.1 _a (3.3)	29.6 _b (4.5)	15	5.9 _a (1.2)	22.1 _b (3.0)	8
<i>Scytonema</i> (%)	2.2 _a (0.8)	2.4 _a (1.0)	15	1.0 _a (1.0)	17.6 _b (6.8)	8

For each genera within a site, different subscripts indicate significantly different means by crust type ($p < 0.05$ in all cases). Numbers in parentheses are 1SE.

Table 2

Statistical table for photosynthesis (P_n), nitrogen fixation (NA), and chlorophyll fluorescence (F_v/F_m) comparisons between early and later successional biological soil crusts from the Colorado Plateau (Canyonlands) and Chihuahuan Desert (Jornada)

Season	Metric	Main effects and interactions	Canyonlands		Jornada	
			(F or χ^2 *)	p	(F or χ^2 *)	p
Spring	P_n	Type	26.95	0.0066	219.92	<0.0001
		Time	16.79	<0.0001	32.77	<0.0001
		Type \times time	1.43	0.2426	10.33	0.0002
	Na	Type	10.39	0.0070	0.52*	0.4698
		Time	20.27	<0.0001	76.29*	<0.0001
		Type \times time	1.05	0.4057	1.96*	0.1649
	F_v/F_m	Type	0.15	0.7174	0.96*	0.3280
		Time	40.54	<0.0001	18.87*	0.0004
		Type \times time	2.94	0.0268	0.72*	0.3946
Summer	P_n	Type	5.42	0.0505	12.81	0.0299
		Time	26.47	<0.0001	41.08	<0.0001
		Type \times time	1.00	0.4483	4.75	0.0320
	Na	Type	6.96	0.0203	0.69*	0.4075
		Time	349.00	<0.0001	70.79*	<0.0001
		Type \times time	27.18	<0.0001	6.95*	0.0084
	F_v/F_m	Type	0.64	0.4553	2.74	0.3274
		Time	17.62	<0.0001	6.28	0.0101
		Type \times time	0.65	0.6629	2.70	0.0969
Fall	P_n	Type	0.25	0.6429	4.48	0.0781
		Time	11.39	0.0001	4.37	0.0144
		Type \times time	0.75	0.5700	1.65	0.2105
	Na	Type	3.80	0.0671	13.36	0.0026
		Time	3.99	0.0068	7.51	<0.0001
		Type \times time	2.28	0.0734	8.08	<0.0001
	F_v/F_m	Type	0.96	0.3833	75.37	0.0010
		Time	17.38	<0.0001	4.27	0.0154
		Type \times time	1.54	0.2393	1.61	0.2213
Winter	P_n	Type	1.97	0.2074	7.33	0.0346
		Time	49.97	<0.0001	5.43	0.0125
		Type \times time	1.23	0.3438	1.34	0.3042
	Na	Type	8.39*	0.0038	40.46*	<0.0001
		Time	40.26*	<0.0001	33.04*	<0.0001
		Type \times time	12.94*	0.0003	52.69*	<0.0001
	F_v/F_m	Type	5.46	0.0683	11.84	0.0388
		Time	3.70	0.0270	4.64	0.0299
		Type \times time	0.67	0.6220	1.96	0.1878

For main effects, Type refers to crust type and Time refers to time of day. Shown are F -test or chi-square (χ^2) values and p values.

Canyonlands (Fig. 1). Repeated-measures ANOVA indicated significant differences in diurnal P_n by crust type at Jornada during all seasons (Table 2). Significant time effects on P_n were also seen in Jornada crusts, with low morning rates during all seasons and midday depression of photosynthesis during summer (Fig. 2). Significant type \times time interactions

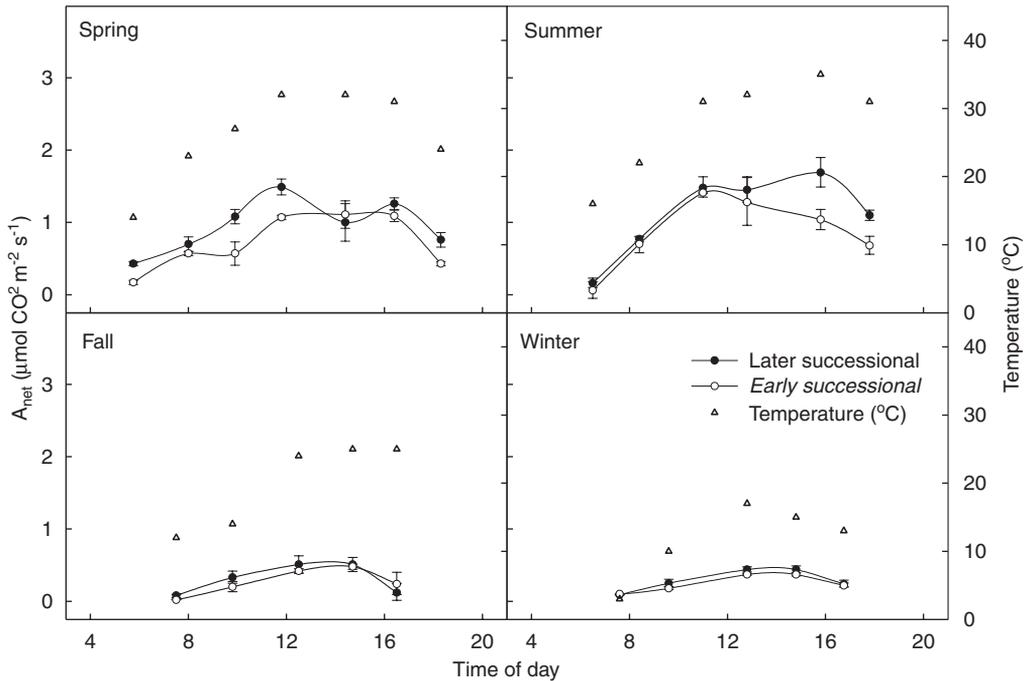


Fig. 1. Seasonal diurnal carbon fixation in early and later successional biological soil crusts from the Colorado Plateau (Canyonlands). Shown are means (\pm 1 SE) and temperatures at time of measurement.

on P_n were seen in the Jornada crusts during spring and summer as a result of greater daily fluctuations of P_n in later versus early successional crusts. Daily integrated P_n was significantly (1.2–1.3-fold) greater for later versus early successional crusts at Canyonlands during all seasons except fall (Fig. 3; Table 3). Jornada later successional crusts had significantly (2.4–2.8-fold) greater daily integrated P_n than early successional crusts during all seasons (Fig. 3; Table 3).

Significant differences in ethylene production indicated greater NA in the later successional crusts at each site. At Canyonlands, repeated-measures ANOVA results indicated NA was significantly greater in dark crusts during all seasons (Table 2). Canyonlands crusts also showed significant effects of time, with ethylene production peaking in the morning hours in all seasons but winter where it peaked in the afternoon (Fig. 4). Canyonlands crust types differed in ethylene production over the diurnal sampling period, resulting in significant type \times time interactions during all seasons except spring. Repeated-measures ANOVA results indicated Jornada NA was significantly greater in later successional crusts during fall and winter, and did not differ by crust type in spring and summer (Table 2). At the Jornada, significant time effects in all seasons again revealed that ethylene production was not static over the course of the day, and was again higher in the afternoon during winter (Fig. 5). Significant type \times time interactions also occurred in Jornada crusts in all seasons except spring, resulting from higher ethylene production in later versus early successional crusts during mid-morning (summer and fall) and midday (winter). Seasonally, later successional Canyonlands crusts had 1.3–7.5-fold higher daily integrated ethylene production than early successional crusts (Table 3, Fig. 6). Seasonally,

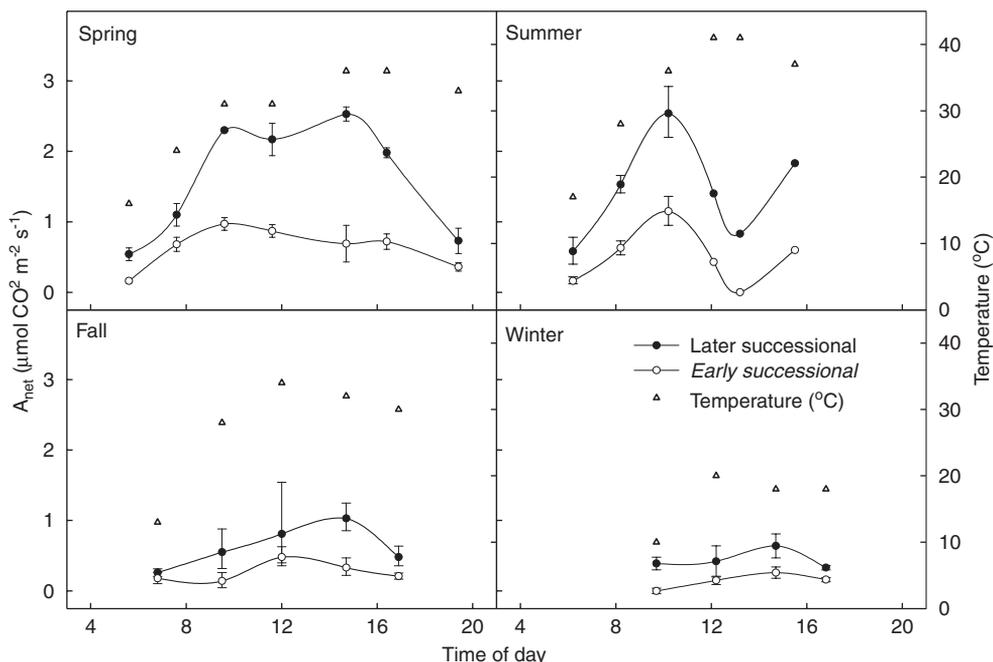


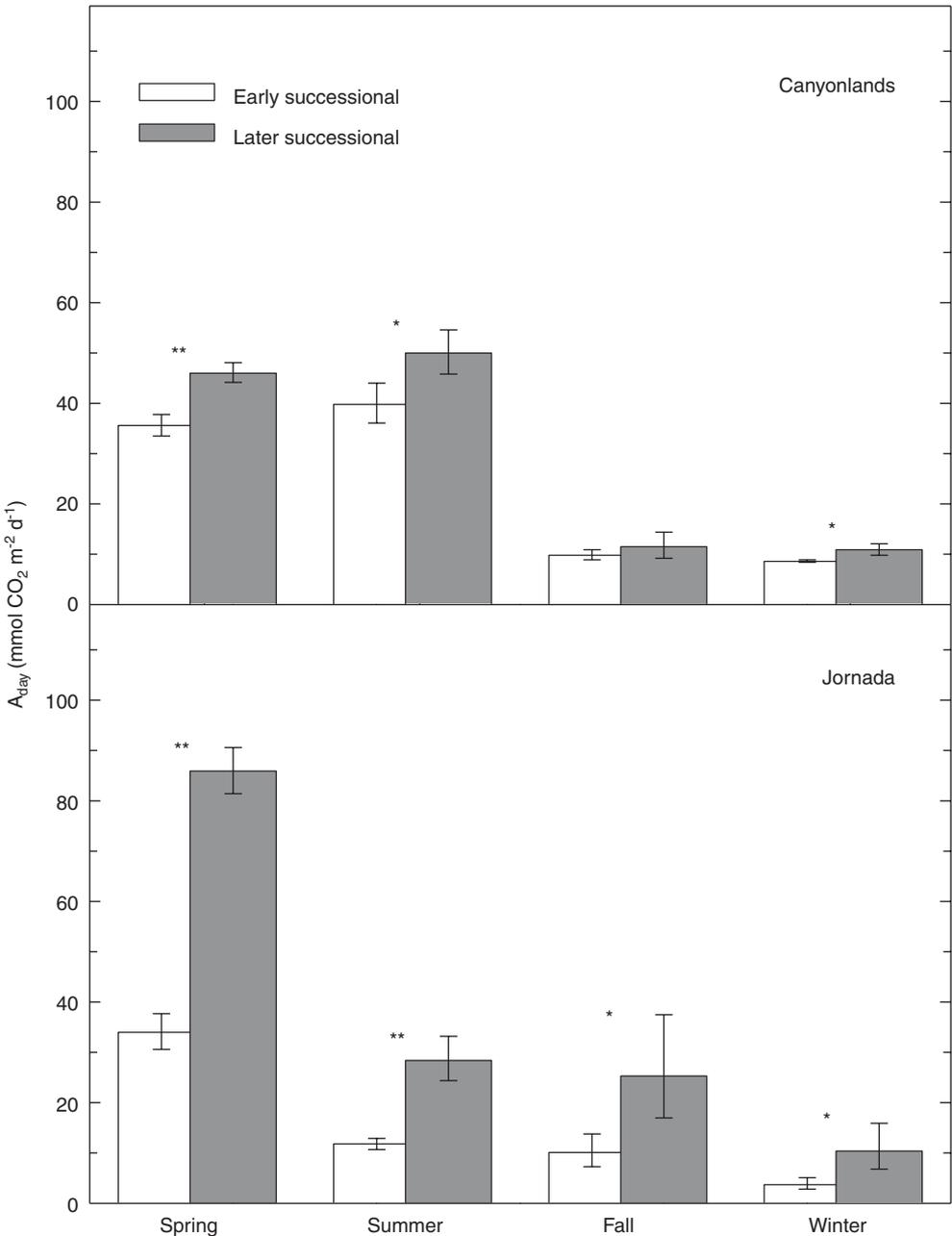
Fig. 2. Seasonal diurnal carbon fixation in early and later successional biological soil crusts from the Chihuahuan Desert (Jornada). Shown are means (\pm ISE) and temperatures at time of measurement.

later successional Jornada crusts had 1.3–25.0-fold higher daily integrated ethylene production than early successional crusts.

Significant differences in chlorophyll fluorescence indicated greater photosynthetic efficiency in the later versus early successional crusts at each site. Seasonally, mean daily F_v/F_m of later successional Canyonlands crusts was significantly greater than that of early successional Canyonlands crusts during winter only (Table 4). At the Jornada, mean daily F_v/F_m was significantly greater in later versus early successional crusts during all seasons except summer (Table 4). For both sites and all seasons, there were significant effects of time of day on F_v/F_m (Table 2), with values increasing through the day except during summer, which showed midday depression of F_v/F_m at both sites. Significant type \times time interactions were also found in Canyonlands during spring and Jornada during fall, both the result of higher F_v/F_m in later successional crusts during early morning and early successional crusts during late afternoon.

4. Discussion

Biological soil crusts are vital contributors to C and N inputs in arid and semi-arid ecosystems of the southwestern US (Beymer and Klopatek, 1991; Evans and Ehleringer, 1993; Evans and Lange, 2003). Plant interspaces were once thought to be unproductive, nutrient-poor microsites that contributed little in the way of ecosystem services. We now know interspaces harbor an array of cyanobacteria, lichens and mosses that may occupy up to 70% of the surface area in the southwestern US (Belnap, 1994), making them a



dominant component of the living cover, and some suggest a dominant component of C and N cycles in drylands (Harper and Marble, 1988; West, 1990). While instantaneous rates of C fixation in biological soil crusts are generally low compared to those of other

Table 3

Statistical results for daily integrated carbon and nitrogen fixation between early and later successional biological soil crusts from the Colorado Plateau (Canyonlands) and Chihuahuan Desert (Jornada)

Season	Canyonlands				Jornada			
	Carbon fixation		Nitrogen fixation		Carbon fixation		Nitrogen fixation	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Spring	3.54	0.0120	12.62	0.0052	7.92	0.0007	1.52	0.0803
Summer	1.72	0.0802	18.25	0.0008	4.91	0.0040	3.48	0.0019
Fall	0.65	0.2768	6.60	0.0234	1.82	0.0713	3.13	0.0037
Winter	2.08	0.0532	33.22	<0.0001	1.97	0.0604	6.82	<0.0001

Shown are *t*-test values and *p* values.

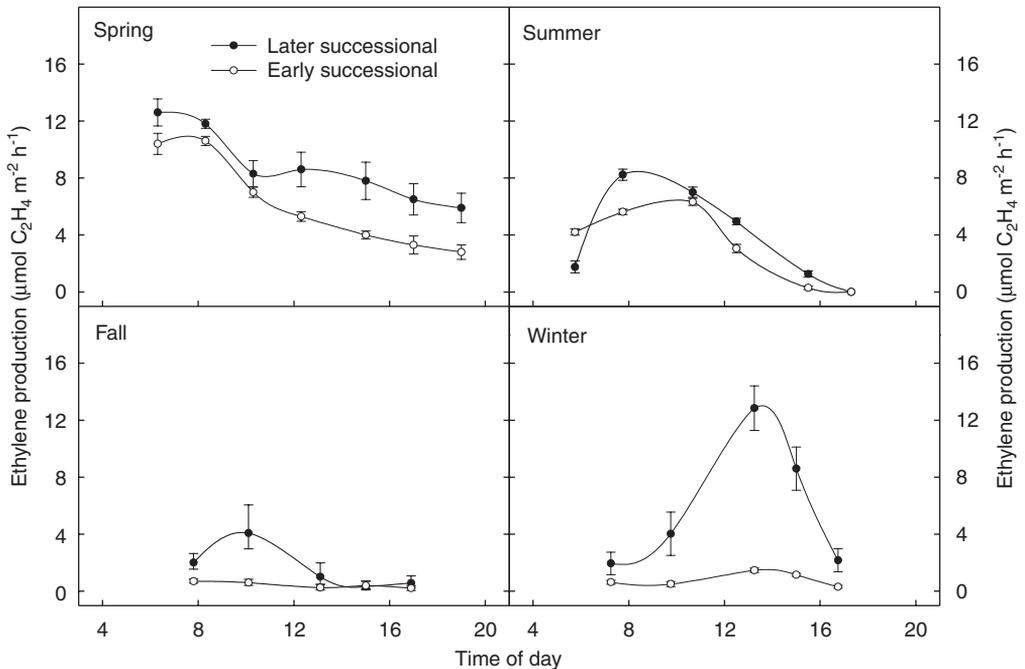


Fig. 4. Seasonal diurnal ethylene production in early and later successional biological soil crusts from the Colorado Plateau (Canyonlands). Shown are means \pm 1 SE.

photosynthetic organisms, the immense surface area they cover results in substantial inputs of C into the landscape. Estimates for annual C inputs by crusts range from 0.4–2.3 g C m⁻² year⁻¹ for early successional crusts to 12–37 g C m⁻² year⁻¹ for later successional crusts (Evans and Lange, 2003). Estimates of N inputs of early and late successional crusts in the southwestern US are 1.4 and 9.0 kg N ha⁻¹ year⁻¹, respectively (Belnap, 2002).

As predicted, we found C and N fixation rates were significantly greater in more developed soil crusts. Later successional crusts at the Canyonlands site had 1.2–1.3-fold

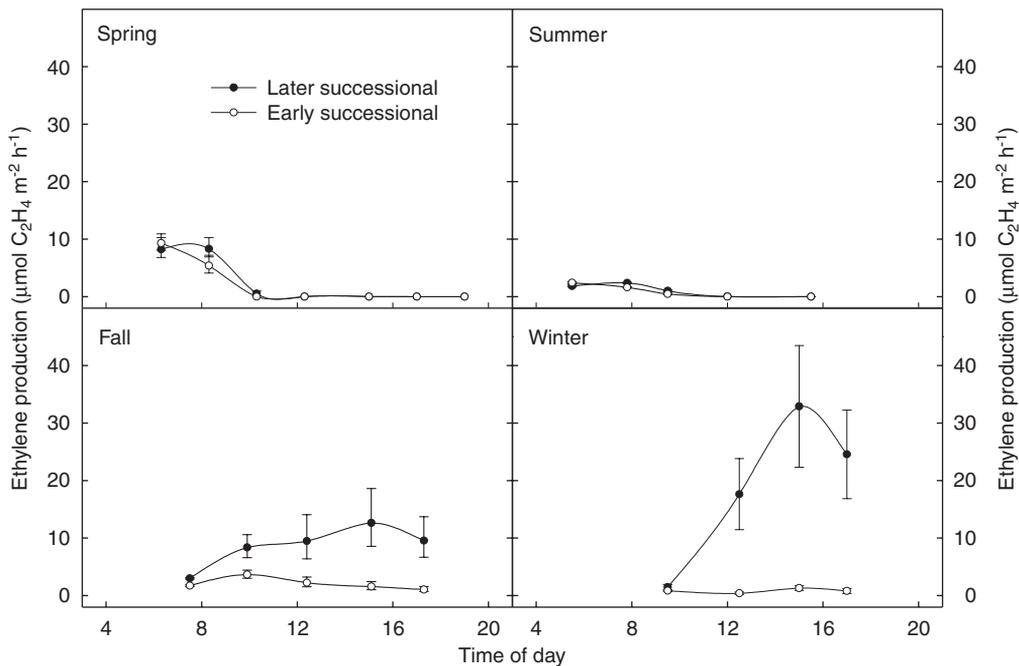


Fig. 5. Seasonal diurnal ethylene production in early and later successional biological soil crusts from the Chihuahuan Desert (Jornada). Shown are means \pm 1 SE.

greater C fixation than early successional crusts, while at the Jornada, later successional crusts had 2.4–2.8-fold greater C fixation than early successional crusts. Similarly, late successional crusts at Canyonlands had 1.3–7.5-fold greater NA than early successional crusts, whereas late successional Jornada crusts had 1.3–25.0-fold greater NA than early successional crusts. Because the N_2 -fixing lichen *Collema* was not included in our NA samples, the values for later successional crusts are conservative estimates. Nonetheless, these findings indicate loss of more developed crusts reduces C and N inputs in these ecosystems.

Our cyanobacterial frequency results support the finding of Yeager et al. (2004) that the higher rates of both C fixation and NA activity in more developed crusts are in part due to an increase in microbial biomass of the later successional species *Nostoc* and *Scytonema*. Our *Nostoc* frequencies averaged 15% and 16% greater in later versus early successional crusts from Canyonlands and Jornada, respectively. In addition, *Scytonema* frequency was nearly 17% greater in later versus early successional Jornada crusts. A ca. 3-fold increase in chlorophyll *a* concentration per g soil in later successional compared to early successional crusts at both sites (data not shown) also supports our finding of greater photosynthetic rates in those crusts.

Our results suggest that photosynthetic capacity of hydrated biological soil crusts can be high in the summer if temperatures are not extreme. Because crusts spend short periods hydrated between prolonged periods of drought, the high net photosynthetic rates we measured during that period suggest they may employ a strategy of rapidly repairing cell damage to achieve net C gain prior to desiccation. Our experiment kept the crusts moist

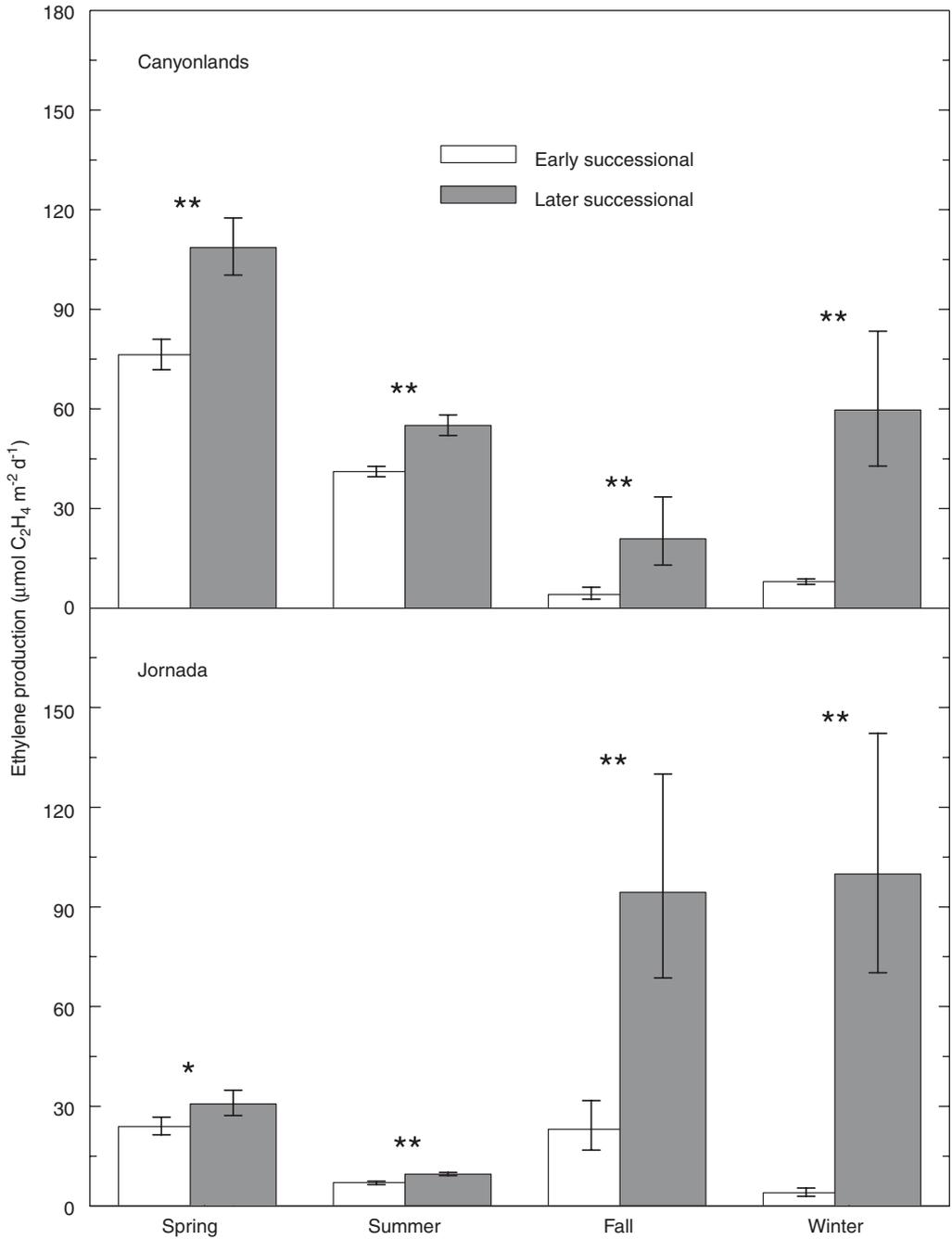


Fig. 6. Daily integrated ethylene production for early and later successional biological soil crusts at Canyonlands (top) and the Jornada (bottom). Shown are means \pm 1 SE. Asterisks indicate significant differences between crust types within a site and season ($p < 0.05^{**}$ or $p < 0.10^{*}$).

Table 4

Mean daily chlorophyll fluorescence (F_v/F_m) for early and later successional biological soil crusts from the Colorado Plateau (Canyonlands) and Chihuahuan Desert (Jornada)

Season	Canyonlands			Jornada		
	Early successional	Later successional	<i>n</i>	Early successional	Later successional	<i>n</i>
Spring	0.268 _a (0.029)	0.274 _a (0.025)	3	0.200 _b (0.014)	0.259 _a (0.038)	3
Summer	0.334 _a (0.023)	0.318 _a (0.018)	3	0.257 _a (0.025)	0.260 _a (0.035)	3
Fall	0.375 _a (0.032)	0.408 _a (0.033)	3	0.320 _b (0.023)	0.529 _a (0.017)	3
Winter	0.323 _b (0.012)	0.423 _a (0.022)	3	0.230 _b (0.043)	0.472 _a (0.027)	3

Different subscripts indicate significantly different F_v/F_m for crust types within that site and season. Numbers in parentheses are 1SE.

for an entire day, a realistic scenario for late fall through early spring. However soils after summer storms typically dry within a few hours, resulting in less C fixation than our measures. Thus, while our daily C fixation values in summer were robust estimates, they nonetheless show the large difference in fluxes between early and later successional stages of soil crust development.

At both locations, diurnal NA typically peaked prior to midday for both crust types, and then declined through the day. This afternoon decrease could have resulted from less-optimal temperatures, or may have been the result of N buildup in the crustal organisms and/or surrounding soils, as such an accumulation is known to slow or stop N fixation (reviewed in [Belnap, 2003](#)). In winter, however, peak NA was not seen until the afternoon, corresponding with temperatures closer to those optimal for N fixation. Nocturnal ethylene production was $< 1 \mu\text{mol C}_2\text{H}_4 \text{m}^{-2} \text{h}^{-1}$ in both sites and crust types during winter (data not shown). Such low activity was expected, as temperatures were near freezing during those measurements. Previously, [Hartley and Schlesinger \(2002\)](#) measured ethylene production rates in a similar Jornada tarbush site at the end of the dry season, obtaining values of $0.01 \mu\text{mol C}_2\text{H}_4 \text{m}^{-2} \text{h}^{-1}$. This was similar to rates we obtained during late summer afternoons when our measured NA rates were the lowest of any season. Overall, however, our potential NA rates were orders of magnitude higher than the aforementioned study. A likely explanation is that the environmental conditions (i.e. water, light, C and N availability) preceding and during measurements have a large influence on NA rates and thus need to be controlled if comparisons are to be made ([Belnap, 2003](#)).

Our F_v/F_m results partially support the hypothesis that later successional crusts have higher maximum quantum yields than early successional crusts. Jornada later successional crusts contained lichens and a greater *Scytonema* cell frequency than Jornada early successional crusts, and typically had greater seasonal F_v/F_m values. This is not surprising, given the fact that the UV protective pigments which protect photosystem II are more abundant in later successional crusts ([Garcia-Pichel and Belnap, 1996](#)). The magnitude and direction of differences in F_v/F_m we observed in Canyonlands crusts were similar to those measured by [Bowker et al. \(2002\)](#) in Colorado Plateau crusts. These differences in F_v/F_m values between successional stages may be due to greater water holding capacity in later successional crusts, since F_v/F_m declines with decreasing water content ([Lange et al., 1989](#); [Deltoro et al., 1998](#)). Likewise, during winter, the darker color of later successional crusts may make them and underlying soils relatively warmer during the cool days compared to

the lighter colored, early successional crusts, leading to more favorable temperatures for photosynthesis and hence greater quantum efficiency.

Soil surface disturbances are increasing rapidly in the southwestern US, converting large areas of later successional *Nostoc/Scytonema* and *Placidium/Collema* crusts to early successional *Microcoleus* crusts. Ecological succession back from early to later successional crusts can take decades to centuries (Belnap and Eldridge, 2003). Increasing temperatures may also reduce crust inputs of C and N due to reduced activity resulting from faster drying soils, and lichen mortality resulting from the higher temperatures (Belnap, Phillips and Troxler, unpublished). Therefore, the combination of increased soil surface disturbance and climate change is expected to significantly diminish the contribution of fixed C and N by biological soil crusts. As Saugier et al. (2001) have estimated deserts cover $27.7 \times 10^6 \text{ km}^2$ and contain $10 \times 10^{15} \text{ g C}$, and Garcia-Pichel et al. (2003) have a conservative estimate of cyanobacterial biomass on these lands to be $56 \times 10^{12} \text{ g C}$ (based on a area of $38.7 \times 10^6 \text{ km}^2$), it seems likely conversion from late successional to early successional crusts will represent a significant loss in C and N pools from these regions.

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